cies interactions (competition, predation, and disease) determine whether a species thrives or withers in a given environment (*10–12*). The final factor is habitat: Cottonwoods grow throughout the southwestern United States, but only along rivers. Which of these factors are most important?

It is becoming clear that the answer depends on scale. Competition is played out at small scales through interactions between individual organisms (birds in this case). It is difficult to imagine how the interaction between two birds can be influential at large scales, and indeed there is evidence that the role of competition drops off to close to zero at biome or nearly continental scales (*13*, *14*). But there is a big gap between small (up to hundreds of meters) and large (thousands of kilometers) scales. Where exactly does competition disappear?

Gotelli *et al*. assembled an impressive data set on the distribution of birds at the scale of a country (Denmark). Based on the evidence and thinking just mentioned, they expected that competition would no longer be influential at this scale, and that habitat (specifically, the varying types of vegetation) would be most important in controlling where bird species live. Surprisingly, they found that habitat appeared unimportant, but that competition was important in determining which bird species lived where.

The results help to put a band on the scales at which competition is important. Gotelli *et al*. show that at the scale of a few hundred kilometers on a side, competition is important, but we already know (*13*, *14*) that at the scale of a biome (roughly 1000 km by 500 km in the two cases studied), competition is not very important (see the figure). This is an astonishingly precise scale-dependent statement of when competition is important and unimportant.

Thus, Gotelli *et al*. provide an example of how ecology can proceed. Rather than debating which of the four forces is most important in general, ecologists need to ask which force (or forces) is most important at a given scale (see the figure).The first step toward identifying scale dependencies of this kind is to collect more data on what controls species distribution and other variables (such as richness, productivity, and abundance) across scales. However, this will lead to many distinct scale diagrams such as that in the figure, one for each variable to be explained. This raises several new challenges and questions.

What is the minimum number of scale diagrams that we need? Can we, for example, collapse the richness-area and richness-productivity diagrams into one? Given that scale is relative to organisms—forces acting at a scale of 1 m are unlikely to be the same for bacteria and elephants—how can we rescale depending on the organism? Another factor is time. It has been suggested that processes that dominate at large spatial scales usually occur over large temporal scales (*2*). Is this true? And can the importance of different processes (the thickness of the bars in the scale diagram) be measured quantitatively? Statistical techniques and nested sampling designs that tell us how much variation occurs in the variable of interest at each scale could help to address these questions (*15*). The answers will help to put ecology on a more quantitative footing.

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ASTRONOMY

Hidden Growth of Supermassive Black Holes in Galaxy Mergers

Changes in the fraction of quasars hidden by gas and dust over cosmic time helps confirm models of the evolution and merger rates of galaxies.

Joel Primack

Black holes are found at the centers of massive galaxies. Although no light escapes from them, their presence can be revealed by the glow of surrounding gases compressed and heated by the driving force of the black hole's gravitation. This quasar emission ranges from low-energy radio waves to the highest-energy gamma-ray region of the electromagnetic spectrum. Quasar formation can be driven by galaxy mergers, which change the distribution of gas around the black hole. This process can also create stars that supernova and create interstellar dust that obscures our view of galactic centers in the visible to x-ray regions. On page 600 of this issue, Treister *et al*. (*1*) present an analysis of data from several space-based telescopes, showing that a greater fraction of quasars that formed in the early universe were obscured by dust, compared with its later stages. This is consistent with observational evidence on the evolution over cosmic time of gas-rich galaxies and a theoretical model for the rate at which they merge.

Like geologists and evolutionary biologists, astronomers reconstruct the past to understand the present. Landforms erode and only a tiny fraction of organisms fossilize, but all of the energy that was ever radiated by galaxies is still streaming through the universe and can be detected in some form. Some of this radiation is altered. For example, redshifting occurs because the wavelengths of photons stretch as the universe continues to expand, and some short-wavelength photons like x-rays and ultraviolet light are absorbed by dust and re-emitted at longer wavelengths. To figure out what happened in the cosmic past, we must see the entire electromagnetic spectrum, from the high-energy gamma rays to the long-wavelength radio waves. Fortunately, NASA's Great Observatories in space cover much of this wavelength range—x-rays (the Chandra X-ray Observatory), near ultraviolet to the near infrared (the refurbished

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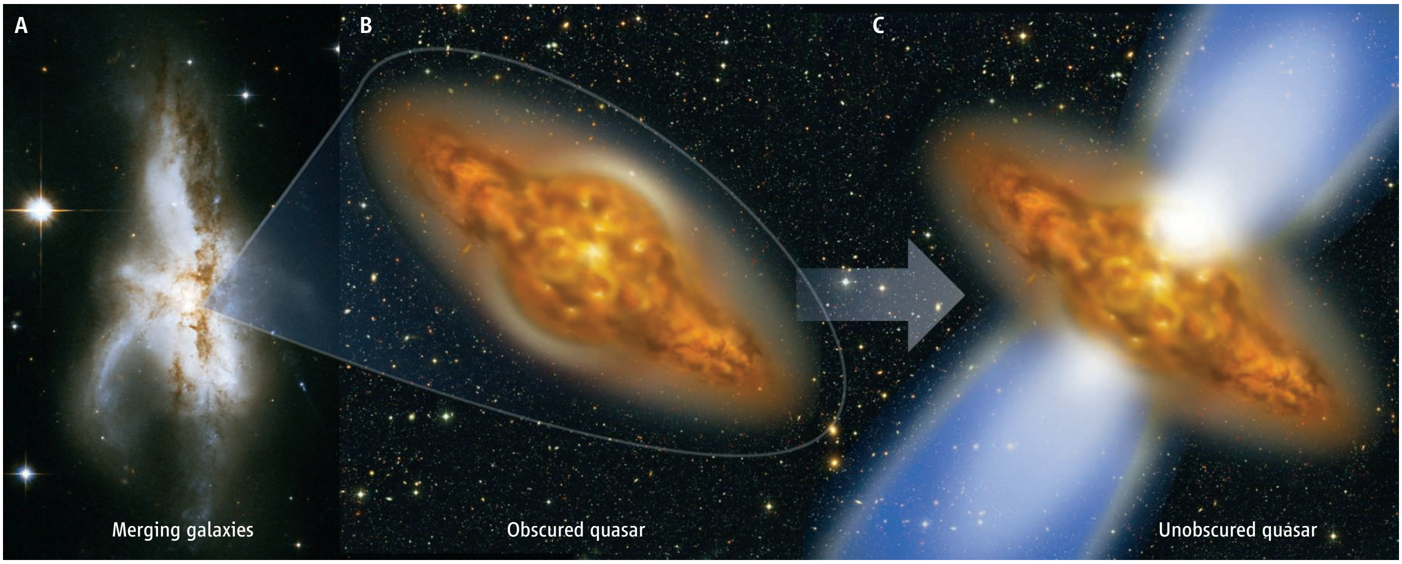

Varying degrees of transparency. (**A**) Galaxy mergers produce quasars (**B**) that are first hidden by gas and dust. (**C**) After about 100 million years, as the quasar radiation blows away the obscuring material, the quasars become visible. The quasar would still be obscured if viewed as seen here, but it would shine much more brightly than the entire galaxy if viewed from some perpendicular directions. The study by Treister *et al.* reveals how the formation of obscured versus visible quasars has changed since the early universe.

CREDITS: (A) GALAXY NGC6240 FROM THE HUBBLE HERITAGE/STSCI/AURA, ESA/HUBBLE COLLABORATION, AND A. EVANS/UNIVERSITY OF VIRGINIA, CHARLOTTESVILLE/NRAO/STONY BROOK UNIVERSITY; (B AND C) ARTIST'S VIEWS: KAREN TERAMURA/INSTITUTE FOR ASTRONOMY, UNIVERSITY OF HAWAII

Hubble Space Telescope), and infrared (the Spitzer Space Telescope).

What we hope to observe is the evolution of both black holes and their host galaxies, and to understand how both black holes and the stellar spheroids in which they are found can increase their masses by a factor of 100 or more during galaxy mergers. The mass of the black hole at the center of our Milky Way galaxy is relatively light, just 4 million times the mass of our Sun, and it resides at the very center of our galaxy's central mass of stars, the stellar spheroid (*2*), from which the spiral arms emanate. Black holes with masses up to billions of times greater than that of our Sun lurk at the centers of massive elliptical galaxies. In all cases, the mass of the black holes is about a thousandth the mass of their host stellar spheroids (*3*).

Black holes can exhaust the local neighborhood of material that feeds them. Some of the gas can be accelerated toward the black hole but may escape entry and shoot away from it at high speed. However, gas can be resupplied to the black hole when galaxies interact and merge (*4*). An example of a galaxy merger with a hidden quasar is shown in the figure, panel A. Computer simulations of such mergers of disk galaxies, which include their massive dark-matter halos, show that they produce elliptical galaxies, with the process sometimes accompanied by spectacular cosmic fireworks (*5*, *6*) (see movie s1).

Gravitational interaction between merging disk galaxies can drive gas into their central regions. The galaxy centers then merge, together with their black holes. The gas fuels gigantic bursts of star formation. Some of the stars produced are an order of magnitude more massive than the Sun. Their supernova explosions at the end of their lives produce great quantities of dust that obscure the galactic centers.

A small fraction of the central gas is accreted by the central black hole as an elliptical galaxy forms. The black hole's mass multiplies by a large factor, and the greater gravitational pull accelerates nearby matter, heating it and causing the radiation we see as a quasar. Late in cosmic time (the part of the universe near us), less than half of such accreting black holes are hidden by the surrounding gas and dust (as in the figure, panel B), whereas the other half shine as quasars in the visible spectrum and as x-rays (as in the figure, panel C). However, in the distant, early universe, the ratio of obscured to unobscured quasars was greater by about a factor of 10, according to observational evidence assembled by Treister *et al.* from the Spitzer, Hubble, and Chandra space telescopes.

These results agree with their modeling studies that use information on how the number of gas-rich galaxies and their merger rate evolved with cosmic time. The merger rate was determined by a large simulation (*7*) based on the Lambda–Cold Dark Matter (ΛCDM) model, the standard one used in modern cosmology (*8*). Most of the cosmic density is in two invisible ("dark") components, dark energy (lambda, about 72%) and cold dark matter (CDM, about 23%). Atomic matter is only about 5%, of which only about 0.5% of the total galactic mass is visible as stars, gas, or dust (*9*).

This agreement between observation and theory shows that the decrease in the fraction of obscured quasars in the nearby (late) universe is a consequence of the decreasing number of galaxies per unit volume as the universe expanded, the decreasing merger rate per galaxy, and the decreasing fraction of gas-rich galaxies as the gas turned into stars. Most of the growth of the mass of the supermassive black holes occurred in the quasar phase, much of it hidden by dust. However, the x-rays from this hidden black-hole accretion should be detectable by new focusing x-ray telescopes, including NASA's NuSTAR satellite (*10*), to be launched in 2011 and to be joined by the Japanese NeXT/Astro-H satellite (*11*) a few years later.

Part of the job of astronomers trying to discover how the universe formed is bookkeeping: counting galaxies of various types in various stages of evolution, both in observations and in increasingly powerful theoretical simulations. It is currently impossible to simulate all of the relevant physical processes, because even the most powerful supercomputers are not yet fast enough, and also because the physical phenomena are not yet understood sufficiently. The most productive approach for now is to simulate the formation of individual galaxies, including mergers, and then use these simulations and observations to guide larger bookkeeping efforts. The resulting semianalytic models attempt to follow the evolution of the entire galaxy population through cosmic time, including the formation of supermassive black holes (*12*, *13*). Fortunately, observations by satellite and ground-based observatories have determined the cosmological parameters with great precision (*14*). The latest cosmological-scale simulations (*15*) are providing a basis for a new round of even more ambitious semianalytic models to be compared with new multiwavelength observations.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/328/5978/576/DC1
Movie S1

10.1126/science.1189695

BEHAVIOR

Cooperation and Punishment

Punishment can support cooperative behavior in a group, but requires coordination.

Louis Putterman

In an era in which the "tragedy of the commons" has acquired new meaning on a global scale, social scientists are beginning to find hope in human nature. True, we are self-interested creatures capable of destroying the habitats that support us as we each focus on getting our share of the global commons before others beat us to it. Yet *Homo sapiens* could never have populated the planet and mastered complex technologies and organizational forms had nature not also made us sensitive to one another's regard. Both field studies and laboratory experiments depict humans as willing to cooperate when convinced that others are doing the same and that at least some will incur costs to sanction cheating. On page 613 in this issue, Janssen *et al.* (*1*) show that communication among members of a group is key to establishing cooperation and using punishment effectively, and on page 617, Boyd *et al.* (*2*) provide a model of how signaling (a stylized kind of communication) could have allowed punishment and cooperation to evolve.

For over a century, economists and social scientists have used the "*Homo economicus*" construct to depict humans as rational beings who act entirely in their own self-interest. Populating their models with *Homo economicus* gave economists the basis for predicting efficient outcomes in market interactions, but it also implied that mutually beneficial cooperation could not occur without binding contracts or outside enforcement. In the prisoners' dilemma game, each of two players has both a cooperative and a selfish option ("defection").

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Achieving cooperation. Coordination is key to successful cooperation. A group in rural Burkino Faso is shown.

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While both would be better off with mutual cooperation than with mutual defection, the fact that the privately best option of each is to defect leads to the prediction of mutual defection, if the game is played once without binding agreements. Still, when real individuals are enlisted to play the game as experimental subjects, with real money at stake, substantial numbers try cooperation.

Related evidence that real individuals are not accurately depicted by the *Homo economicus* model came from experiments using the voluntary contribution mechanism, a variation on the prisoners' dilemma game, in which each individual can choose not only full cooperation or no cooperation, but also intermediate levels of cooperation in the form of contributing funds to a collectively advantageous group project. The first voluntary contribution mechanism experiments defied the *Homo economicus* prediction of universal "free-riding," finding instead that many players did contribute to the common good rather than defect by contributing nothing. But when the game was played repeatedly for a preannounced number of times, contributions fell off toward zero. However, a result frequently replicated in the last decade shows that when subjects are permitted to communicate before playing or are allowed to punish one another's actions, conditional cooperation trumps strict self-interest (and *Homo sapiens* triumphs over *Homo economicus*) (*3*).

In different ways, Janssen *et al.* and Boyd *et al.* address the same problem. Permitting costly punishment often leads to more sustained cooperation, and the willingness to incur a cost to punish is characteristic of *Homo sapiens*. But uncoordinated punish-